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INHERITANCE OF NUMBER OF FEATHERS OF THE FANTAIL PIGEON

PROFESSOR T. H. MORGAN
Columbia University

Several years ago I began to study the inheritance of the number of the tail feathers in fantail pigeons, partly because of a challenge that I would not recover the fantail in the F_2 generation, the implication being that the inheritance was not Mendelian. The race of fantails is a very old one and the pigeons have been very intensively selected by fanciers for many years. It was therefore to be expected that several modifications had in time been accumulated in the direction of selection. Nevertheless, it was to be expected that if a sufficient number of individuals were bred, the original type would reappear. If two factors in homozygous condition are essential for the reappearance in F_2 of the original fantail, then such an individual is expected once in sixteen cases; if three factors, once in sixty-four cases; if four, once in two hundred and fifty-six; if five, only once in 1,048 cases, etc. This relation holds if the fantail factors are all recessive, but fewer factors are called for if one or more of them is dominant, and the question will be still more complicated if the highest reaches of the variation are due to modifying factors acting only in the presence of other factors.

It seemed unlikely, however, that the situation would be found to be as simple as this; for, in the first place, there is no fixed number of tail feathers characteristic of

the fantail; selection of these birds has not been made exclusively in regard to number of feathers, but in regard also to their size and shape, their regularity of distribution, their method of spreading, etc. It was a priori unlikely that the race itself is homozygous for *all* of the factors that influence the number of feathers. How far the results would depend on whether the maximum effects are produced by a homozygous condition in several of the factors, with heterozygous condition in others, would be a point not easy to ascertain in a race that produces as few offspring as does the pigeon. Nevertheless, the results give, I believe, pretty clear indications that the effects are due to several factors, and they indicate, moreover, that the failure to recover the extreme type of the fantail in F_2 is probably only a question of insufficient numbers—in fact, the fantail type has probably reappeared in F_2, though not in its most extreme form, even with the relatively few F_2 pigeons that I have been able to get.

The work has extended over several years, owing to lack of suitable quarters in which to keep the birds and of assistance to take care of them. They had to be removed to and from Woods Hole each year, with the consequent loss of young and disturbance of the regularity of habits essential to a bird as conventional as the pigeon.

The original stock was obtained from Dr. F. D. Solley, of New York City, a well-known breeder of high-grade fantails. Dr. Solley has also supplied me with information as to the number of tail feathers in birds of his strain. Unfortunately these numbers were not obtained until a year after these particular birds had passed out of his hands. He assures me they are typical, and the birds of his stock that I saw when my parent birds were obtained were closely similar in tail number, etc., to those here recorded.

The birds with which the original fantails were bred to get F_1 stock were ordinary birds. As they were not pedigreed stock there is a small chance that they might have contained factors of the fantail type, but this is

highly improbable, since they had the number of feathers characteristic of nearly all other strains of pigeons, and especially of the more common ones.[1] Three P_1 pairs were used (two male fantail and one female) but the F_1 individuals were not kept apart (for want of space) and, as no marked difference appeared amongst the F_1 progeny when the fantail parent was female or male, the F_1's from the reciprocal crosses were mixed together. This is unfortunate, for fuller and more accurate observations might have revealed significant differences indicative of sex-linked factors. I can only state that if such are here involved their effect is slight, and was not observed at the time when the two kinds of F_1 offspring were reared.

History of the Fantail Race

In his book on "Animals and Plants under Domestication" Darwin has given a great deal of important information about the origin and characteristics of the fantail.

"The normal number of tail feathers in the genus *Columba* is 12; but fantails have from only 12 (as has been asserted) up to, according to MM. Boitard and Corbie, 42. I have counted in one of my own birds 33, and at Calcutta Mr. Blyth has counted in an *imperfect* tail 34 feathers. In Madras, as I am informed by Sir W. Elliot, 32 is the standard number; but in England number is much less valued than the position and expansion of the tail. The feathers are arranged in an irregular double row; their permanent fan-like expansion and their upward direction are more remarkable characters than their increased number. The tail is capable of the same movements as in other pigeons and can be depressed so as to sweep the ground. It arises from a more expanded basis than in other pigeons; and in three skeletons there were one or two extra coccygeal vertebræ. I have examined many specimens of various colors from different countries, and there was no trace of the oil gland; this is a curious case of abortion.[2] The neck is thin and bowed backwards. The breast is broad and protuberant. The feet are

1 At least one other of the domesticated races may have more than twelve feathers in the tail.

2 "This gland occurs in most birds; but Nitzsch (in his 'Pterylographie,' 1840, p. 55) states that it is absent in two species of *Columba*, in several species of *Psittacus*, in some species of *Otis*, and in most or all birds of the Ostrich family. It can hardly be an accidental occurrence that the two species of *Columba* which are destitute of an oil gland have an unusual number of tail feathers, namely 16, and in this respect resemble fantails."

small. The carriage of the bird is very different from that of other pigeons; in good birds the head touches the tail feathers, which consequently often become crumpled. They habitually tremble much; and their necks have an extraordinarily, apparently convulsive, backward and forward movement. Good birds walk in a singular manner, as if their small feet were stiff. Owing to their large tails, they fly badly on a windy day. The dark-colored varieties are generally larger than white fantails."

"Mr. Swinhoe sent me from Amoy, in China, the skin of a fantail belonging to a breed known to have been imported from Java. It was colored in a peculiar manner, unlike any European fantail; and, for a fantail, had a remarkably short beak. Although a good bird of the kind, it had only 14 tail feathers; but Mr. Swinhoe has counted in others of this breed from 18 to 24 tail feathers. From a rough sketch sent to me, it is evident that the tail is not so much expanded or so much upraised as in even second-rate European fantails. The bird shakes its neck like our fantails. It had a well-developed oil gland. Fantails were known in India, as we shall hereafter see, before the year 1600; and we may suspect that in the Java fantail we see the breed in its earlier and less improved condition." Vol. I, Chap. V, p. 153.

"The first notice of the existence of this breed is in India, before the year 1600, as given in the "Ayeen Akabery"; at this date, judging from Aldrovandi, the breed was unknown in Europe. In 1677, Willighby speaks of a fantail with 26 tail feathers; in 1735, Moore saw one with 36 tail feathers; and in 1824, MM. Boitard and Corbie assert that in France birds can easily be found with 42 tail feathers. In England, the number of the tail feathers is not at present so much regarded as their upward direction and expansion. The general carriage of the bird is likewise now much valued. The old descriptions do not suffice to show whether in these latter respects there has been much improvement; but if fantails with their heads and tails touching had formerly existed, as at the present time, the fact would almost certainly have been noticed. The fantails which are now found in India probably show the state of the race, as far as carriage is concerned, at the date of their introduction into Europe; and some, said to have been brought from Calcutta, which I kept alive, were in a marked manner inferior to our exhibition birds. The Java fantail shows the same difference in carriage; and although Mr. Swinhoe has counted 18 and 24 tail feathers in his birds, a first-rate specimen sent to me had only 14 tail feathers.[3]

A later statement in regard to fantails from Fulton's Book of Pigeons gives some additional details.[4]

[3] Darwin, ''Animals and Plants,'' Chapter VII, p. 218.

[4] ''The Illustrated Book of Pigeons with Standards for Judging,'' by Robert Fulton, edited by L. Wright. Cassell & Co., Ltd., New York.

The tail also is peculiar, and quite uncommon. It is long and composed of 14 to 22 feathers, 16 being about the average number in these birds; these are arranged equally on either side, one above another, and the two top ones, diverging a little outwards, show a slight division in the tail, but there is not the slightest affinity or resemblance to a "fan" tail, as some might suppose by the excessive number of feathers, but it is a distinct peculiarity of this breed (12 being the normal number of tail-quills in most pigeons). The greater the number of quills in "Oriental Rollers" the more the specimens are valued. A further singular feature noticeable in the tails of these birds is that occasionally two feathers may be found growing from one quill, separating at its pithy junction as a twin feather, each rather narrower than ordinarily, but of the usual length, and not outgrown, or causing a disordered formation of the tail (p. 195).

. . . The tail is the other chief point in the English breed. The feathers should lie flat and evenly over one another (none of them being set edgeways), so as to form a neat double row. In number they should not be less than 28, but as many more as the bird can carry nicely. The Birmingham Columbarian Society, in an article published by them some years ago, laid down 40, arranged in 3 rows, as the proper number; but though I have heard of such birds I have never seen one. I once had a hen with 38 tail-feathers. I purchased her from Mr. Fulton, and I believe she had been imported from India; and I have often bred birds with tails of 36 or 37 feathers carried in most orthodox fashion. In an exhibition pen the number is of no consequence, provided that the tail is well spread and circular, and well filled up all around; but in the breeding pen a thickly-feathered tail is of great value. In the breeding of any animal for any fancy point, if you can get that point in excess in either of the parents so much the easier is your task. You have then something to *spare,* instead of something to breed up to, which is a very different matter (p. 329).

The P_1 Generation

The three original fantails had 29, 30 and 32 tail feathers, respectively (Fig. 1). From Dr. F. D. Solley I got the records of other fantails of the same stock given in Fig. 2. The other parents were ordinary homers purchased from a breeder of these birds.

The F_1 Offspring

The numbers of tail feathers shown by the 41 individuals of the F_1 generation are recorded in Fig. 3. The range of variation is from 12 to 20, with the highest fre-

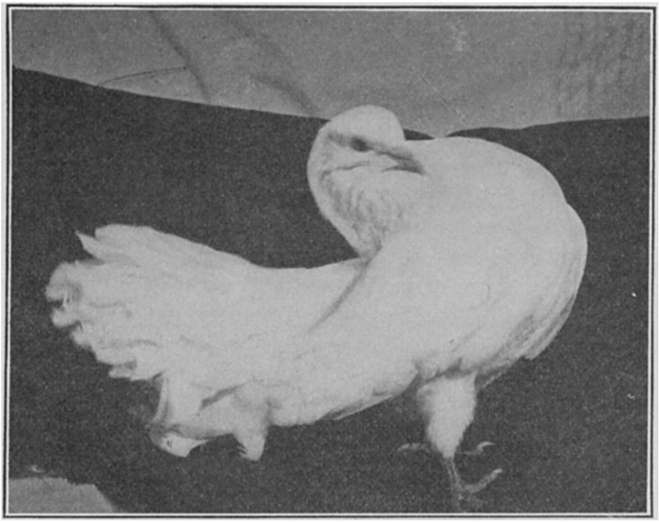

FIG. 1. One of fantail pigeons used in the experiments.

quency in the 14-tail-feather class. Evidently one or more of the factors of the fantail act as partial dominants, producing tails that have for the most part more tail feathers than has the common pigeon but less than the fantail. In appearance these F_1 birds are more like the common pigeon, having lost the peculiar carriage

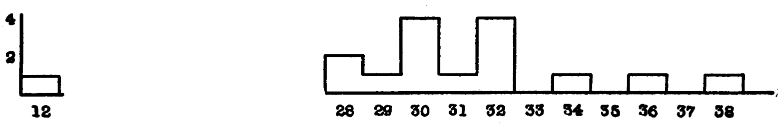

FIG. 2. Frequency distribution of tail feathers in parent "homers" (left), and fantails (right).

FIG. 3. Frequency distribution of tail feathers in F_1.

of the fantail and its peculiar shape. The tail is, however, often wedge-shaped instead of flat as in ordinary birds. There were 28 birds with an even number of

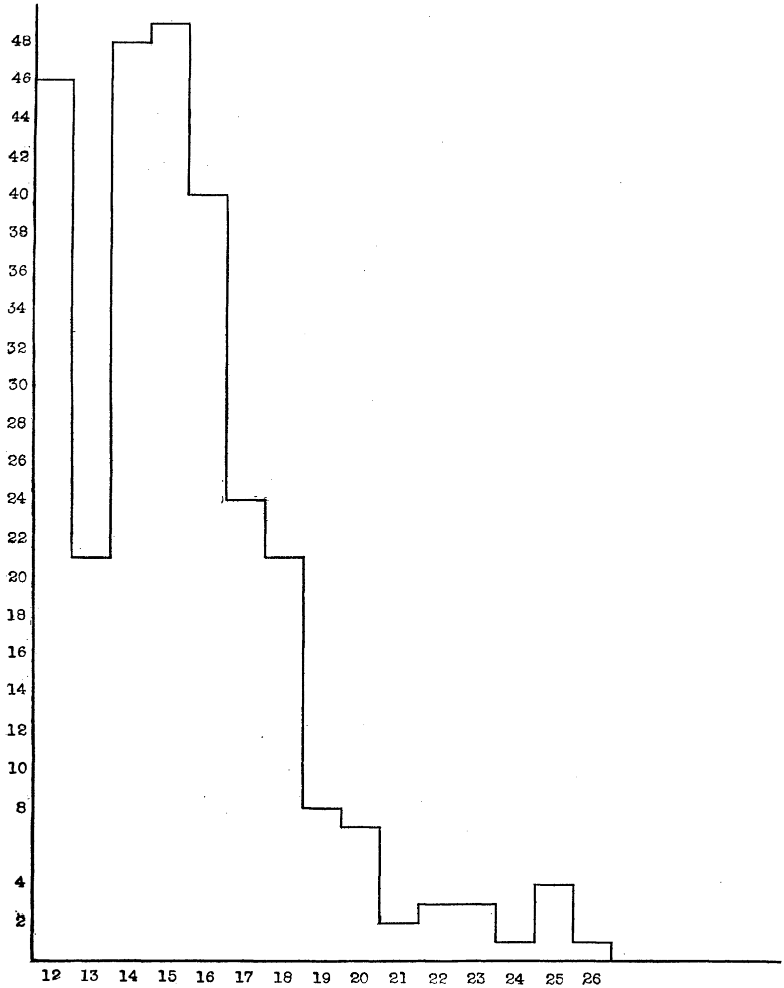

FIG. 4. Frequency distribution of tail feathers in F_2.

feathers and 13 with an odd number—a considerable preponderance of even number of feathers. Of the 41 individuals, 30 are included in the classes with 14, 15, 16 tail feathers.

THE F_2 GENERATION[5]

A glance at Fig. 4 shows that the range of variation of the F_2 group is greater than that of the F_1; that the 12-feathered tail has reappeared in considerable numbers; that the "curve" is at least bimodal with one apex in the 14, 15, 16 rows, and the other in the 12 row; that there are a few individuals that approach the lower range of variation of the fantail, viz., those with 24, 25 and 26 tail feathers.

There is a distinct return of one of the grandparental types, viz., the 12 class. The 13–16 groups clearly correspond to a large part of the heterozygous group seen in F_1. Whether the range to the right of this middle group in the F_2's is significantly different from that in the F_1 can not be determined by inspection, as the number of individuals is too small. If the F_1 and the F_2 groups are made into curves the results show that it is doubtful if the wider range in F_2 is significant, although the large 12-feathered class in F_2 makes the F_2 variability much more marked than the variability in F_1.

BACK CROSS

Some of the F_1 birds, both males and females, were back-crossed to fantails. Twenty-three offspring were obtained which differed strikingly as a group from the F_1 and F_2 lots. The number of tail feathers (Fig. 5) was greater; no 12-feathered birds appeared (the lowest num-

FIG. 5. Frequency distribution of tail feathers in back-cross.

ber was 14); while the highest number included birds with 30 and 31 tail feathers. The latter would undoubtedly pass-for-fantail, so far as the number of tail feathers was

[5] There are some discrepancies between the F_2 and back-cross tables given here and the records of the groups given in "The Mechanism of Mendelian Heredity." The present account is more accurate, as some of the former data was obtained from the birds while still alive.

concerned. The carriage of most of the birds was noticeably much more like the fantail than that of the F_1 and F_2 birds.

Number of Factors Involved

The recovery of a certain number of the normal 12-feathered tail in the F_2 might seem to furnish a basis on which to calculate the number of factors involved; but the fact that a few 12-feathered birds appear in F_1 shows that some, at least, of the heterozygous combination are included in the F_2 twelve feather group. It is also possible, even probable, that other F_2 combinations may also fall within this group. It is impossible, therefore, to arrive at anything more than a possible conclusion from the F_2 data because the relative value of the heterozygous classes can only be guessed at.

Two factors will obviously not fit the results, because there would be expected more of the higher numbers of tail feathers both in the back cross and in the F_2 count. Three factors fit fairly well. Let A, B, C represent partially dominant factors for fantails, and a, b, c their normal allelomorphs (aabbcc being the normal 12-feathered tail). In the F_2 there will be expected only one pure fantail out of 64 (viz., AABBCC) and one *pure* 12-feathered type (viz., aabbcc). There will be six F_2 classes with only one dominant factor heterozygous for A or B or C. These, theoretically at least, if all the factors have equal efficiency, would be the most likely ones to fall within the 12-feathered group. If these include all of the expected 12-feathered tails in F_2 there should be seven 12-feathered in 64. There were 278 F_2 individuals. On the same calculation this would give an expectation of only 10.5 twelve-feathered tails. But the F_2 records actually gave 46 normal tails. Obviously still other combinations realized in F_2 must come under this class. It would be mere guesswork to try to state which are the more probable combinations.

The back cross furnishes data that permit a better means of calculation. Here eight kinds of germ cells and eight

zygotes are expected on the assumption of a three-factor cross, viz.,

ABC	ABc	Abc	aBC	abC	aBc	abc
abc	abc	abc	abc	abc	abc	abc

Of these eight kinds of individuals, some of only one class, might be expected to be wild type (viz., of class abcABC) in the sense that individuals of this class correspond in formula to the F_1 offspring, and, of these F_1 offspring, 2 out of 41 have tails with 12 feathers, or 1 in 20. Amongst the 24 back crossed individuals, there were none with 12 feathers only and at most one is expected. If we assign to the group of abcABC also the four individuals of the back cross in the 14 and 16 groups, and assign the 3 individuals of the 30 and 31 groups to the pure fantails, there remain 17 individuals in the middle range that belong to the six intermediate groups that are homozygous in one or in two fantail modifiers. There are six intermediate classes between the end classes just spoken of. If we are right in the limits assigned to the end classes, the expectation would be 18 individuals for the intermediate classes, where 17 are so classified, which is also not a bad fit.

Four factors fit the data about as well as three,[6] but if three will suffice the smaller number is perhaps preferable. It is evident that the data do not allow close analysis, but only because they are not sufficiently large, especially in the back cross. Nevertheless, it is important to find out that, so far as the results go, they are not unconformable with the Mendelian assumption of segregation of a few pairs of factors.

LINKAGE

When all F_2 tails that are blue are classified they fall into the groups shown in Fig. 6; similarly, the white tails

[6] On this assumption relatively fewer fantails are expected in F_2, which is a better fit, but fewer also in the back cross, which apparently is not so good a fit. The proportion would also depend, however, on the relative efficiency and the completeness of the dominance of each factor. The above evidence proves that there must be at least three factors.

give the groups shown in Fig. 7. A comparison of these groups shows that there is a relatively large number of high-feathered tails amongst the whites, while among the

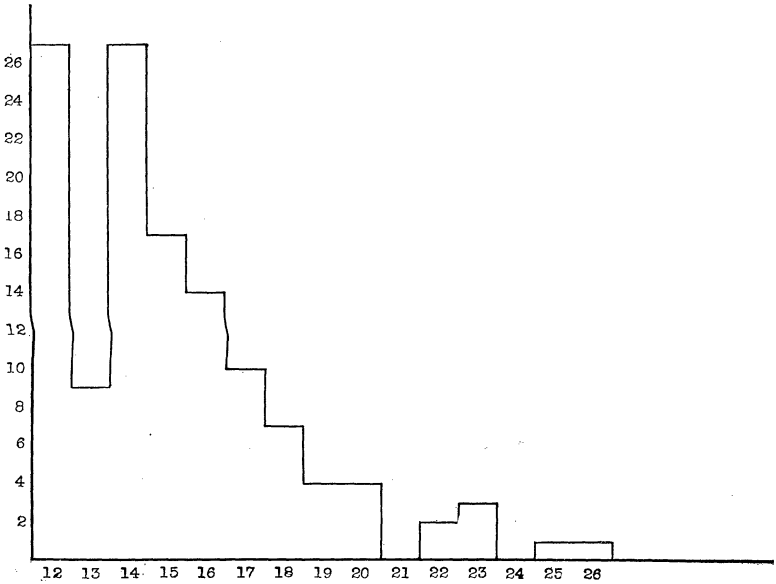

FIG. 6. Frequency distribution of blue tail feathers in F_2.

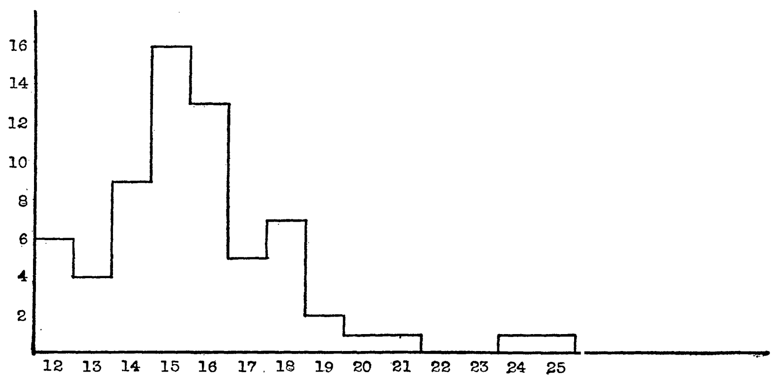

FIG. 7. Frequency distribution of white tail feathers in F_2.

blues, the 12-feathered tails are relatively more frequent. A not improbable interpretation of this relation is that the principal factor for white is linked to one or more of the factors for increased number of feathers.

Since these results occur in the F_2 count, it is unfortunately not possible to deduce from them whether crossing over takes place in one or both or neither sex.

Amongst the tails were some that had both blue feathers and white feathers. These give the group shown in Fig. 8, which closely corresponds to the blue-tail group (Fig. 6). There were other tails with white feathers having

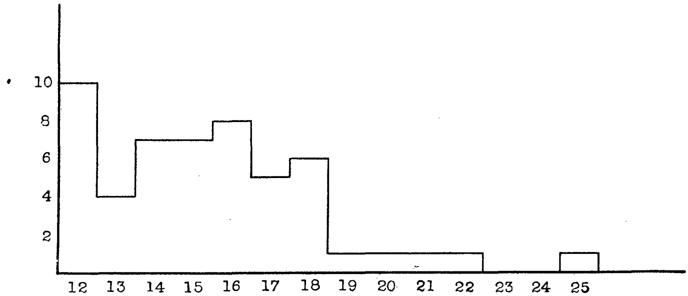

FIG. 8. Frequency distribution of blue-and-white tail feathers in F_2.

pigment along the margins as in Fig. 15. These, when classified, gave the group shown in Fig. 9, which apparently is the same as the group of white tails (Fig. 7).

The number of birds in the F_1 and in the back cross are too few to give significant results when broken up into the two groups of white or blue.

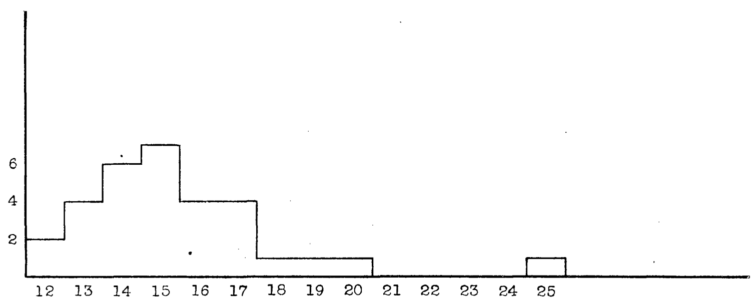

FIG. 9. Frequency distribution of "edged white" tail feathers in F_2.

The tails are not a complete index of the bird from which they came, for a bird with a pure white tail might have color patches elsewhere on its body; but as no rec-

ords were kept of the entire color of each bird, it is not now possible to find out how closely the complete pattern would correspond with the tail color. In general, however, in these birds the tail is a partial index, at least—a fair sample, perhaps—of the entire color.

"Correlation" between the Oil Gland and the Number of Tail Feathers

Darwin suggests a "correlation" between the absence of the oil gland and the increased number of tail feathers. Such a relation might be a direct correlation in the sense that the overdevelopment of the tail feathers suppresses or tends to suppress the development of the oil gland that is situated on the uropygium just above the base of the tail feathers. If this were the true interpretation of the condition in the fantail, one would expect to find in F_1 and F_2 all degrees of development of the oil gland. If, on the other hand, the absence of the oil gland is an inherited peculiarity having nothing directly to do with the number of feathers, then in the F_2 series we might expect to find a numerical relation indicating its mode of inheritance. Unfortunately the pedigrees of the normal tailed pigeons that had been mated to the fantails were unknown. While the oil glands may be occasionally absent in domesticated pigeons, it is highly improbable that any of the homers used in the experiment carried such a factor. In classifying the F_1 and F_2 birds according to the condition of the oil gland three classes were recognized. First, "double" glands, those with the right and left sides almost separate, each with a separate opening; second, "single" glands, those with the halves united more closely and with but one external outlet;[7] third, those with no oil glands. The results are given in graphs of Figs. 10–11.

The few F_1 birds available when the oil gland was studied show a wide range of variability; all but one were double, Fig. 10 (above). This doubling might be due to

[7] An intermediate stage was also noted, viz., one with two closely fused so as to make almost a single gland.

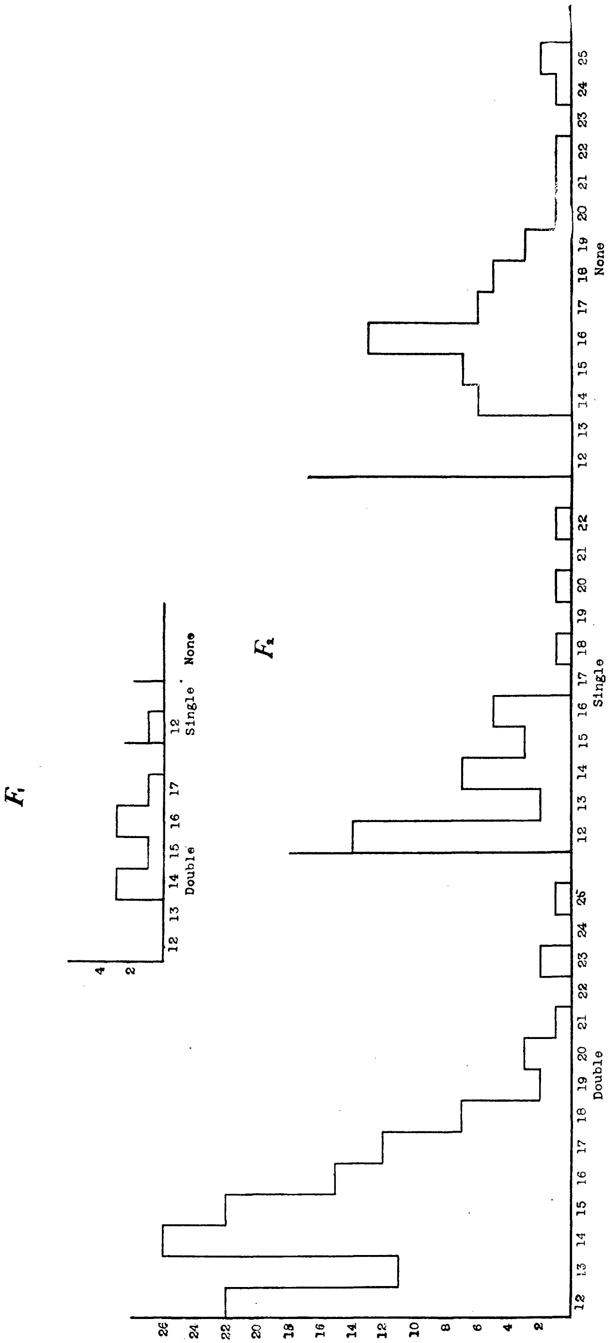

FIG. 10 (above). FIG. 11 (below). Frequency curves of occurrence of oil glands in F_1 and F_2.

partial dominance of a gene for doubling, or to a "correlation" such as Darwin spoke of, for the number of tail

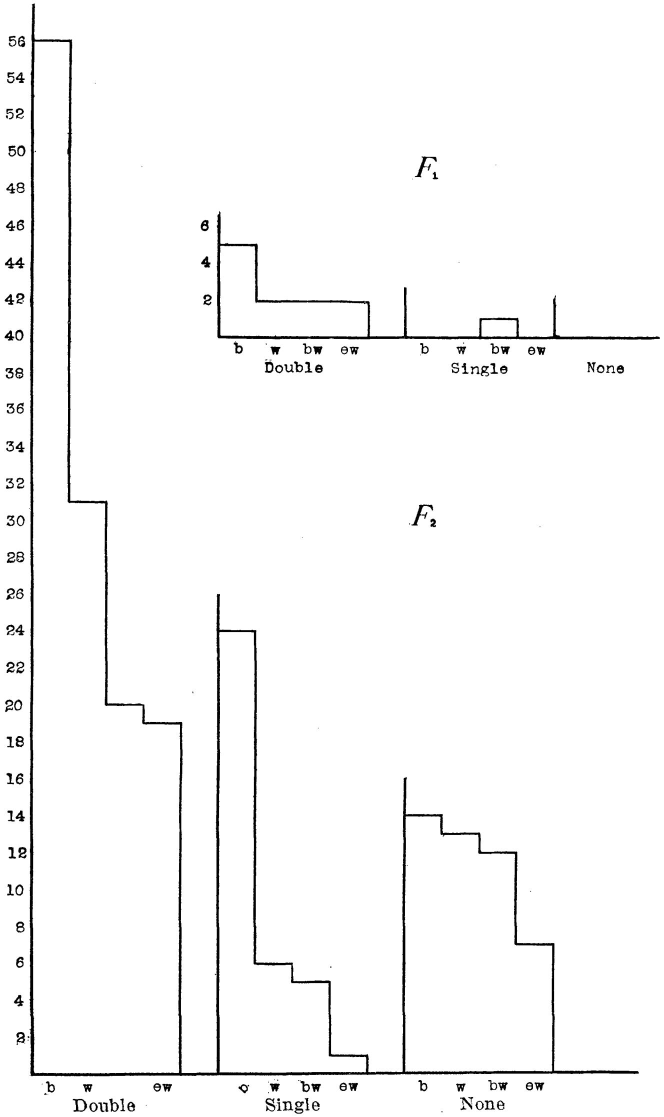

FIG. 12 (above). FIG. 13 (below). Frequency distribution of double, single and no oil glands in differently colored tails.

feathers in this particular lot was high. That the latter is probably not the explanation is shown in the F_2 birds.

The three groups of F_2 tails (Fig. 11) show 126 doubles, 36 singles, 46 none. The expectation for two factors (9:3:4), on the assumption that the doubles differ from the singles by one factor, and both from none by another factor, is 117 doubles, 39 singles, 52 none. This is not a very bad fit.

There is one striking result brought out by these curves. There are no 12- or 13-feathered birds without an oil gland. This is an expression of the relation that Darwin suggested as due to "correlation" in the sense that more tail feathers suppressed the development of the oil gland. But there is no such obvious solution as is shown by the F_2 group, for there may be a large number of tail feathers present and the oil glands be well developed, single or double. The curves suggest, rather, linkage between a gene for extra feathers, and a gene for absence of oil glands.

The tails with double, single and no oil glands were also classified according to the four color groups already referred to, viz., blue, white, blue and white, edged white (Figs. 12 and 13). The double and single curves appear to be the same, the no oil gland curve seems significantly different. If so, it means that there is some linkage between white color and absence of oil glands.

The foregoing evidence makes probable the view that a gene for more than 12 feathers, and the gene for no oil gland, and a gene for white color are linked, *i. e.*, are carried by the same chromosome. The genes for the oil gland and for the number of tail feathers are closer to each other than either is to the gene for white. More data, especially from back-crosses, will be necessary to establish this conclusion.

Split Feathers

Dr. Solley tells me that the split and double feather that occurs at times in the fantails is selected against. It is of not infrequent occurrence in the F_2 and back-crossed birds that I have obtained. In the records these

split feathers have been counted as *one* feather, without, however, intending to prejudice the question of the single or double nature of these feathers.

The most striking cases are like those represented in Fig. 14 (top row) and Fig. 15, where what appears to be

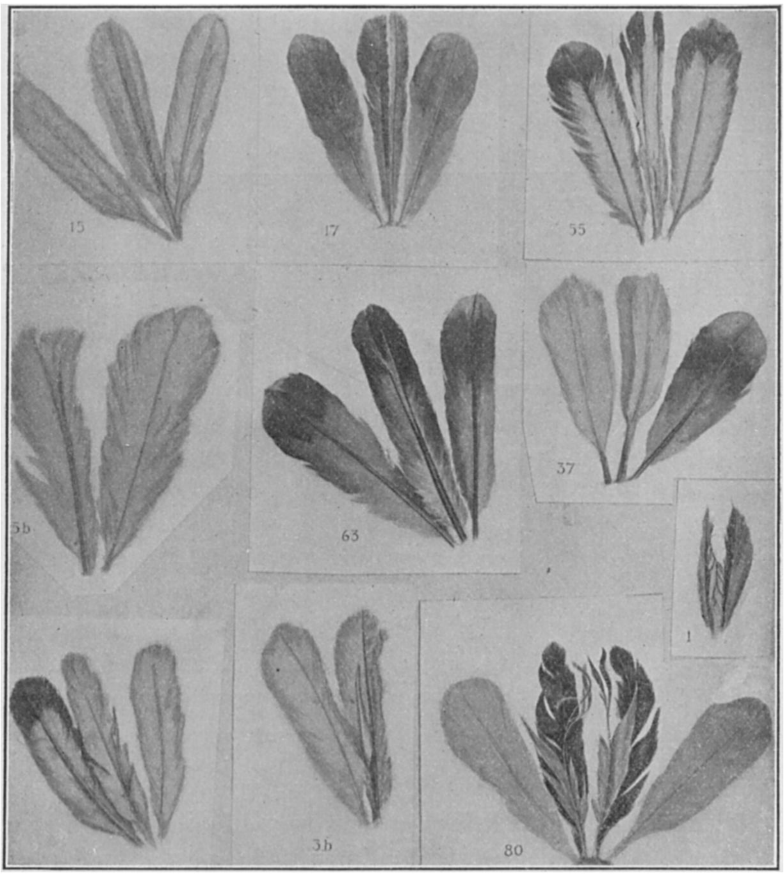

FIG. 14. Some types of split feathers.

a single feather is split in two throughout its length. While there may be a complete shaft in each half, yet the two vanes that lie on the "inner" side are not so broad as the outer half vanes, and their edges are generally frayed out and imperfectly formed. Often the vanes run across and unite the two halves.

In some of the split feathers, the division is obviously into right and left halves (Figs, 14, 15, 16); in other cases the halves make an angle with each other (Fig. 14, Nos. 37 and 80), while in still others one larger part may lie above a smaller part (Fig. 14, lowest row). Whether in the last cases the division has been in a horizontal plane, and in the first cases in a vertical one, is not certain, although the shape of the feathers even in the last case, with the imperfect edge and a narrower margin, would seem to make most probable the view that in all cases the division

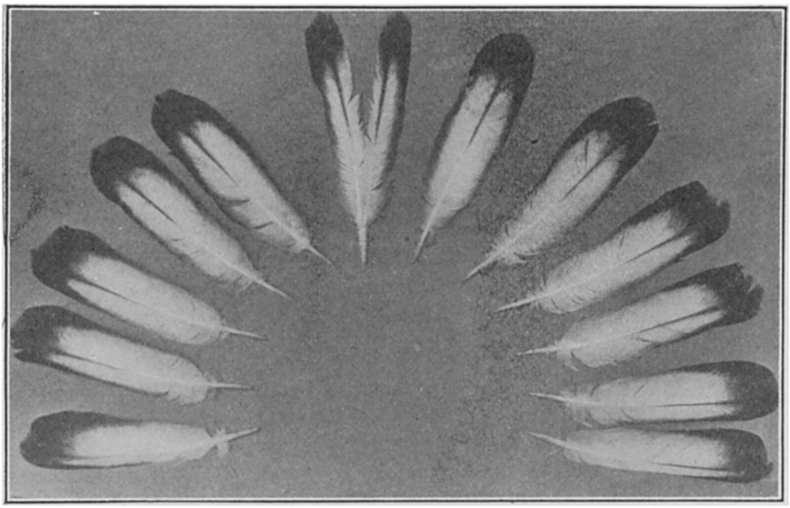

FIG. 15. An F_2 tail ("edged white") with one split feather.

has been into morphological right and left halves. The final position of the feather halves may be due to a later twisting in the sheath, or to crowding of the feathers at the base. This interpretation is further substantiated by cases in which the center of all the feathers has a white area (Fig. 14, No. 55, and Fig. 15); this is found on the imperfect side of the split feathers even when they lie one above the other. In all there were 24 F_2 tails with split feathers. Five of these had each two split feathers.

These cases grade into those in which only the distal end of the feather is split, as shown in Fig. 14, middle figure, and Fig. 16. The impression produced by feathers

of this kind is strikingly in favor of a single feather split into right and left parts at the distal end. In all, three cases of this sort were found.

To the same group are to be referred two cases, one of which is shown in Fig. 14, No. 5, *b*. Here there is a single feather, but the midrib is split near the end. The vane

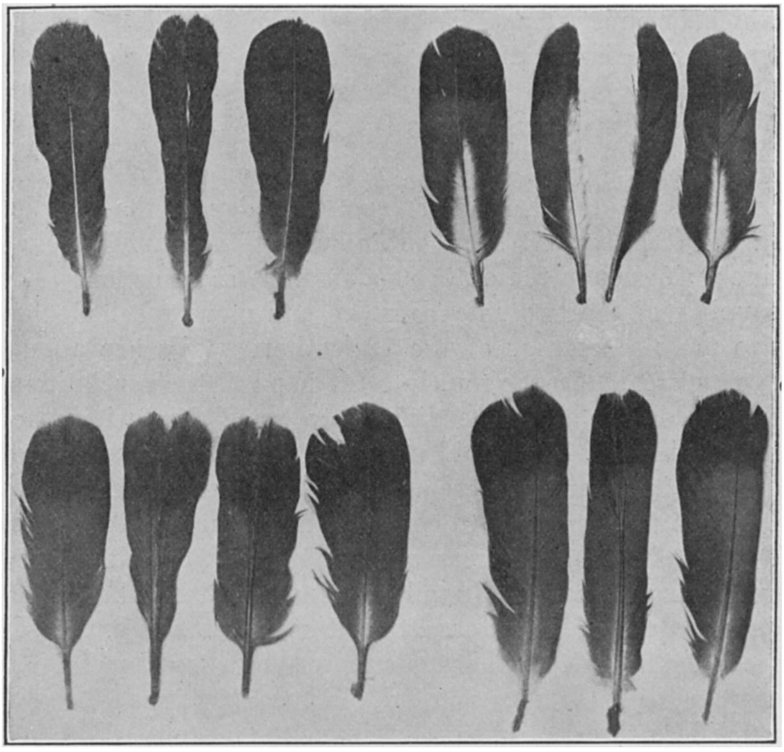

FIG. 16. Split feathers with normal feathers that lie next to them.

lying between the two midribs is continuous, yet the bending inwards of this part is indicative of its dual nature.

More extreme are the eight cases of which three are shown in Fig. 16, lowest row. In all such cases there is a large, almost fully formed feather with a smaller, less perfect piece *underneath* the larger part. The first impression is that a piece has been split off the ventral side of the feather by a division in the horizontal plane. A

closer scrutiny shows, however, that the large feather is ragged along one edge only (or on a part of one edge), while the smaller piece has also on the same side (as can be seen in some cases at least) a ragged edge with the other vane more nearly complete and with a not-rough edge. It seems, therefore, more reasonable to interpret even these cases as extremes of the split-feather type in which one piece has fared worse than the other (or in which the original division was into unequal pieces).

THE SIZE OF THE DOUBLE FEATHERS

There is a graded difference between the outer and inner vanes of the feather from the edge to the middle of the tail Fig. 15. The outer half of the vane is relatively smaller in the outermost feather, right or left, and equality of the two sides is more and more reached, the two middle feathers of the 12-feathered tails are about symmetrical. In the multiple feather tail these relations still hold, but are more difficult to trace than when the tail is simpler. It would not be profitable to attempt to analyze in detail these relations as applied to the double feathers further than to compare their surface relations with that of the feathers nearest to them or with their symmetrical mates. In all cases of split feathers the outer halves of the vanes are not so wide as is expected from the nearest feathers (or their symmetrical mates as seen in Figs. 14–16). The middle part is, as a rule, very much less than a right or left vane. The total width of the split feather is, as nearly as I can judge, about the same as the expected feathers for that position. The impression indicates that the sum of the four vanes is a little greater than the sum of the two normal vanes, but there can not be much difference as measurements show. The looseness of the frayed inner edge makes it difficult to get a very close estimate of the actual relations.

The general conclusion is that we are dealing with a single rudiment that has split at a very early stage into two parts that have completed themselves as whole

feathers, so far as this intimate union in the middle line of the bud permitted. There are no indications that the split feather is due to the union of two separate rudiments that have been pressed together so closely as to interfere with the full development of each when they came in contact.

The Location of the Split Feathers

The location of the split feathers (and modified types) is given in the next table.

Feather "split"	9 near middle,	1 one quarter from side
End only split	2 near middle,	1 one third from side
Double vein at tip	2 near middle	
Very unequal parts	7 near middle,	1 two thirds from side, 1 outermost feather.

In the great majority of cases the doubling occurs near the middle of the tail. The meaning of this is not at all apparent. We know so little about the cause of duplication in general and about the embryological mechanism that is involved in laying down the feathers in the tail, that it is useless to speculate about the result. The evidence from experimental embryology shows unmistakably that doubling may result from a mechanical interference with the relation of the blastomeres after they have assumed a definite position in regard to each other, but there are also many other cases known where, in normal development, a part is repeated several or many times. In these cases we can as yet only surmise that the rudiments of the structure—simple cells or groups of cells—become mechanically drawn apart by the more rapid growth of surrounding parts and separated so that each gives rise to a separate organ. Split feathers, from this point of view, would be looked upon as an incomplete separation of certain of the rudiments. However this may be, one can imagine other ways by which a specialized group of cells could become broken up into islands.

Other Characters in the Cross

Three other characters are conspicuously present in the fantails besides the tail, viz., the white plumage, the carriage of the bird, and the shaking of the head and neck. The dominance—incomplete—of the white of the fantail was noted,[8] but the mixtures that appeared both in F_1 and F_2 make it probable that the results are not due to a single factor. The extraordinary position of the fantail pigeon with its head thrown back until it touches the tail feathers appears also to be due to at least as many factors as is the number of feathers in the tail; for it was not recovered in any of the F_2 birds, although in the back cross there were birds that showed some approach to the fantail posture. The shaking of the head disappeared in F_1 and indications of it were seen occasionally in F_2 and especially in back crosses. The character is of such a kind that its study is difficult, and it may well be an expression of some structural modification of the body rather than any direct psychological factor.

Castration of Male

The absence of marked secondary sexual characters in the male, characters that are so conspicuous in many other birds, suggested the possibility that here, as in the Sebright male fowl, the suppression of the male plumage might be due to substances developing in the testes. Unlikely as this seemed (because pigeons with diseased testes would probably have occurred and any change recorded), nevertheless I tried the effect of castration on one young F_2 male that was just weaned. Some feathers were removed at the same time. The bird was kept for about five months and did not show any change in its plumage. It appears probable, then, that there are no genetic factors in pigeons, like those in the Sebright, which, acting through the testes, suppress the development of the plumage in the male.

[8] See Cole *et al.*

REFERENCES

Browne, R. Staples.—On the Inheritance of Color in Domesticated Pigeons with Special Reference to Reversion. *Proc. Zool. Soc. London,* 1908.

Bonhote, J. L. On the Inheritance of the Webfoot Character in Pigeons. *Proc. Zool. Soc. London,* 1911.

Bateson, W. Mendel's Principles of Heredity. 1913, p. 36.

Morgan, T. H. Notes on Two Crosses between Different Races of Pigeons. *Biol. Bull,* XXI. 1911.

Morgan, T. H., Sturtevant, A. H., Muller, H. J., and Bridges, C. B. The Mechanism of Mendelian Heredity. New York, 1915, p.

Cole, J. A Case of Sex-linked Inheritance in the Domestic Pigeon. *Science,* XXVI, 1912.

Darwin, Chas. Animals and Plants under Domestication.